BOTANICAL GAZETTE

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A comparative study of the roots of Ranunculaceæ.

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WITH PLATES II—IV.

(Continued from p. 16.)

II. Methods of investigation.

I began collecting material for this work in August, 1891, and continued collecting until the ground became frozen in the fall. The roots of Ranunculaceæ being generally fibrous, and often very long and slender, it was no easy matter to obtain material that would answer my purpose, as in all cases I desired perfect root tips for the study of the meristem, besides pieces of the root from several points in its length for the comparative study of the general structure. Of many of the species I obtained plants which were potted and after getting them started in a cold frame they were placed in the green house, and when more material was needed I had but to take the plant from the pot, disturbing it as little as possible, and then repot it to keep for farther use. My best sections were obtained in this way, for after the plants became thoroughly established the root tips were abundant and there was not the danger of injuring them in collecting which necessarily attends out-door collection of such material. Another advantage from this method was that they were always ready at hand when more material was needed to corroborate some point. The material was all dehydrated and hardened in alcohol, a Thomas dehydrating apparatus being used. It was then prepared according to the collodion method, in all cases serial longitudinal sections of the root tip being made for the study of the meristem. Over three hundred slides were prepared, about two hundred of which furnished the material for my study. The roots of some of the plants were so small that the making of good sections was a difficult task. Among such roots are those of *Anemone Caroliniana, Coptis* *trifolia*, and *Anemonella thalictroides*. Many of these roots which were sectioned were less than .5^{mm} in diameter. Sectioning such roots met with many failures, especially in getting good longisections of the tip. One series of transections of a root the diameter of which could not have been over .25^{mm} was obtained, which showed the bundle structure fairly well. Careful camera lucida drawings were made of the transections of most of the roots, and these with the sections of the roots themselves were studied in making my comparisons. All of these drawings could not be embodied in this thesis, but many of them will be found on the plates. In the study of the meristem structure rough drawings were made of most of the tips, then comparisons were made, and but one detailed drawing was made for each type of structure.

III. General structure.

As to the general histological structure, especially as to the difference between old and young roots, I should make two general classes of the plants of Ranunculaceæ, first, those not showing decided secondary change in older roots, and second, those presenting certain modifications from the primary structure in the older roots; in the second class there are two different modifications of the primary structure, thus making three classes.

The first class includes those plants in which the original radial structure persists in the older roots, that is secondary growth produces but little change in the plan of root structure. The cortex may become less compact by the disappearance of cells, and the xylem may increase in the number of its rays, and its vessels in the number and thickness of their walls, but the primary radial structure is still evident. As especially good representatives of this class I would name the roots of *Ranunculus septentrionalis* and *Ranunculus acris*. In these the smallest branches and the largest main roots showed exactly the same type of structure. This plan for *R. acris* is shown in plate II, figs. 5 and 6. In both of these plants the oldest roots showed in the bundle area simply an increase in the number of the xylem vessels, and in the cortex irregular air spaces occurred through the disappearance of cells in certain areas or the tearing apart of the cells through rapid growth, but the plan of structure was still the same as in the younger roots, this being a triad or tetrad radial bundle. In this class I would also include *Hepatica acutiloba*,[1] *H. triloba*, *Aconitum Noveboracense*,[2] *Trollius laxus*, *Caltha palustris*,[3] *Ranunculus recurvatus*, *R. Pennsylvanicus*, *R. fascicularis*,[5] *R. circinatus*,[6] *R. aquatilis* var. *trichophyllus*,[7] *R. bulbosus*, *R. multifidus*,[8] *R. septentrionalis*, and *R. hispidus* Michx.,[9] a form not recognized as a distinct species in Gray's Manual, but it is certainly a very distinct type and I believe is recognized as a species by many botanists, though others regard it as a variety of *R. fascicularis* or *R. septentrionalis*. In root structure it is more like the latter. In all of these species which I could get to study, the roots, both young and old, large and small, had the characteristic radial type of root structure. In certain cases it might be that at another time of the year the roots would have presented a different structure, though as most of my material was collected in the fall the larger roots collected then ought to have shown it, if there was to be a change through secondary growth.

The second class on this basis would include those plants in which, by the growth of secondary xylem rays between the primary ones and in front of the phloem masses (these secondary rays often becoming more prominent than the primary ones), the radial character of the young root is lost and the bundle appears like a collateral one with the xylem collected in the center and the phloem in separated groups answering to the original number of the xylem rays, and lying entirely without the xylem mass. Along with the change in the bundle area the endodermis generally undergoes a change. Through division the cells become much smaller and often nearly square in form; and the whole central cylinder becomes larger in proportion to the diameter of the root, partly through increase in bundle elements and partly through increase of conjunctive parenchyma. On the other hand many of the roots of the first class show a smaller central cylinder in the older roots, the increase principally having taken place in the cortex.

As a good example of this second class of roots, I will des-

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[1]Plate III, figs. 13, 14.
[2]Plate IV, figs 22, 23.
[3]Plate III, figs. 17, 18.
[5]Plate II, figs. 9, 10.
[6]Plate II, figs. 3, 4.
[7]Plate II, figs. 1, 2.
[8]Plate II, figs. 11, 12.
[9]Plate II, figs. 7, 8.

cribe the two forms of structure as found in the young and old roots of *Clematis Virginiana.*[10] In the young root (fig. 25) the are as marked *x* are the primary xylem rays and *ph* the phloem masses, the cells of which are not drawn, the endodermis is seen at *en*, the cortex at *c*, and the epidermis at *e*.

The structure of the older roots is represented in fig. 24 in which the original xylem rays are at *x*, and secondary xylem rays, *x'*, have been developed so as to be more prominent than the original rays, and have pushed the phloem, *ph*, toward the endodermis; at *a* is what appears to be meristematic tissue, peripherad of which are the phloem cells. All within the dotted line is of thick walled cells, probably a part of the secondary xylem. The endodermis has become somewhat modified though not as much so as in many of the roots of this class, but the central cylinder is notably larger in proportion than in the smaller roots, as the figures well show.

About the same change in structure between the old and young roots is shown in plate IV, figs. 26 and 27, which were drawn from sections of the roots of *Cimicifuga racemosa.* Here the primary xylem and phloem have a tetrad arrangement, but practically the same secondary change has taken place in the older roots and as the lettering is the same the figures will need no explanation. In this class also belong *Anemone Virginiana*[11] and its var. *alba*, *A. Pennsylvanica*, *Actæa alba*,[12] *A. spicata* var. *rubra*, *Clematis verticillaris*, *Coptis trifolia*, *Hydrastis Canadensis*, and *Ranunculus sceleratus*. The structure of the younger roots of *Anemone Virginiana* and its var. *alba*, and of both species of *Actæa* are found represented in the figures. In all, the secondary changes are very similar to those already described, and need no detailed description. The only singular thing about this class is that we find *Ranunculus sceleratus* here, for it is the only *Ranunculus* that shows marked secondary change. As it is reckoned by Dr. Gray as an annual, we should hardly expect a change to occur here, while the roots of *Ranunculus acris*, which is certainly a perennial, do not show secondary change.

I should make a third class of structure for *Thalictrum dioicum*, *Thalictrum polygamum*, *Anemonella thalictroides*, and *Aquilegia Canadensis*, for the larger roots of these plants

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[10]Plate IV, figs. 24, 25.
[11]Plate III, figs. 15, 16.
[12]Plate III, figs. 19, 21.

present a very peculiar structure, as compared with the structure of the roots of the other plants of the order. I will endeavor to make this clear by describing the structure of the older roots of *Thalictrum dioicum.*[13] The smaller, younger roots of all of these plants show the usual radial root structure, and do not deserve particular description. This plant, and especially *Thalictrum polygamum*, has a numerous cluster of large fibrous roots, and it is the structure of these roots that will be described. A cross section of these roots shows a very large central cylinder enclosed by a very regular endodermis composed of very small square cells. The xylem vessels are in a rather compact cluster at the center, and radiating from this are from two to four rays of phloem, each ray of two or more separated groups, the cells of which are very small and thin walled. Sometimes the central xylem presents the same number of short rays as the phloem The greater mass of the central cylinder is occupied by very regular and generally angular cells, the walls of which are often slightly thickened. The cortex is very small in proportion to the central cylinder and is of roundish loosely packed cells. At first an epidermis is present, but most of these roots gathered in the fall had exfoliated their epidermis together with all but about two rows of very loosely packed cortex cells. This leaves the endodermis as the real protecting organ, and perhaps accounts for its rather peculiar appearance. The walls of the endodermal cells are generally cutinized.

The structure of a younger root of *T. polygamum* is shown in plate III, fig. 20 and plate IV, fig. 28. The style of structure which has been described for the older roots of *T. dioicum* was also observed in the older roots of *T. polygamum* and *Aquilegia Canadensis*, and in the tuber-like roots of *Anemonella thalictroides*, though with minor differences in each case. I have not examined the roots of *Isopyrum biternatum*, but from Prof. Hargitt's description I should say it too belonged in this class.

From the above descriptions it will be seen that Olivier's statements concerning the genus *Ranunculus* are borne out by my observations, for in only one species, *Ranunculus sceleratus*, could I discover any great change of structure through secondary development. The exfoliation of the cortex of the Thalictrums is spoken of by both Olivier and Ma-

[13]Plate IV, fig. 29.

rie, though I had made out these facts for myself before knowing what their statements were. Marie also refers to the two forms of structure as found in roots like those of *Actæa alba*.

IV. Miscellaneous considerations.

Treub, among others, proposed to use anatomical characters to aid in the classification of plants, using root characters as well as those of the stem and leaf. Erickson in discussing this idea said that he did not think this could be accomplished, for his study showed him that very nearly related plants showed very different histological structures, and that in many roots which he studied he could not tell the one from the other. From my study of the roots of the *Ranunculaceæ* I should say that anatomical characters, especially root characters, could only be used in a very general way, for I think these vary more according to environment than according to specific relations, and much change of structure is seen in the roots of the same species, especially between younger and older conditions of it. With a few orders and genera, and perhaps species, it is possible that some anatomical character might be found which would be an aid in classification, but I am certain that among the *Ranunculaceæ* I could not tell the difference between the roots of many of the genera; and as to species I should be entirely at a loss to characterize them by root structure. I emphasize the fact that environment influences structure more than specific relations. For example, all the plants of *Ranunculaceæ* inhabiting wet places, no matter of what species, presented in transection rounded cortex cells, and these loosely packed, the spaces between the cells being numerous and varying in size and number in almost direct proportion to the aquatic or terrestrial habit of the plant. On the other hand, plants of very dry ground generally showed angular cortex cells and almost invariably few and small spaces between them. Another difference noted was that the roots of water *Ranunculaceæ* present a poor development of the vascular system, its office probably being filled by the more abundant spaces between the cells, especially in certain roots in which many of the spaces are continuous cavities surrounded by cells. These differences are well illustrated in plate II, figs. 1 and 3, and plate III, fig. 19. Figs. 1 and 3 represent the roots of *Ranunculus circinatus* and *R. aquatilis* var. *trichophyllus*. Both of these grow in water, and we find that the cortex cells are round and have many spaces between the cells, while fig. 19 represents the roots of *Actæa alba*, which grows on dry banks, and here the cortex cells are angular and the spaces between cells are almost none. The differences in vascular development are also well shown in these figures.

In this part of the paper I have not discussed the general structure of the species studied as regards the occurrence and distribution of the histological elements, since I find that Marie, Hegelmaier, and others have described the general structure of many species of *Ranunculaceæ*, and in many cases my descriptions would have been but a repetition of theirs.

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Flowers and insects. X.

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STEIRONEMA LANCEOLATUM Gray.—The plants are commonly collected in small patches. They grow 3 or 4^{dm} high, and expose a few yellow flowers with reddish-purple centers. The flowers look outwards and a little downwards, and expand from 20 to 25^{mm}. In the bud each corolla lobe enfolds an anther. When the flower expands, the lobes carry the enclosed anthers with them, holding them while the stigma is receptive and is exposed to insects—a fact to which my attention was first called by Professor Pammel. After the anthers are released, the styles are commonly found bent outwards, out of the way of the falling pollen. Sprengel supposed that flowers of *Lysimachia quadrifolia* were nectar bearing, but failed to find nectar. He, and Müller also, failed to find honey in flowers of *L. vulgaris*. According to Kirchner nectar is wanting in *L. nemorum* as well as in *L. nummularia*. I have been uncertain in regard to the occurrence of honey in Steironema, but the visits of male bees seem to indicate its presence, although these insects might search for it in vain. They commonly fly about the flowers to find the females, not trying to find honey.

I have noted the flowers in bloom from June 20th to July 12th. As far as I have observed, they are visited for honey and pollen only by *Macropis steironematis* Rob. ♂♀.